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Distributional Ecology of Shallow Southwestern

Beaufort Sea [Arctic Ocean) Bivalve Mollusca

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(Running head: Beaufort bivalve ecology)

Submitted - 12 Aug 83

ABSTRACT

Benthic macrofauna was sampled off the northern coast of Alaska to determine whether the shallow arctic sublittoral fauna is uniformly distributed among stations as suggested by MacGinitie (1955), or whether it is distributed in ecological assemblages. During the study 5000 living individuals were collected of 31 species. Analysis of the bivalve molluscs revealed that there are no general patterns of total numerical density, species richness, or species composition from 5 to 25 m depth across the southwestern Beaufort Sea. There was, however, a greater similarity of bivalve faunal composition among stations than would be expected by stochastic processes alone. An analysis of feeding types demonstrated that there is a tendency toward functional groupings of suspension and deposit feeders. Sedimentary features (interacting with depth) appear to influence the bivalve fauna: more deposit feeding bivalves are associated with finer sediments at the deeper stations. The relatively high species richness in shallow arctic waters more closely resembles bivalve assemblages in protected temperate environments than it does those of the open coast. The lack of major disturbance of sediments by waves in the ice-dominated Beaufort Sea appears to be ecologically important.

INTRODUCTION

Until the last decade the molluscan fauna of the Beaufort Sea was little studied. The few early works were mainly taxonomic: Dan (1919) reported on the molluscs from the Canadian Arctic Expedition (1913-1918). George MacGinitie (1955) and Nettie MacGinitie (1959) published on the molluscs in the Chukchi Sea-Beaufort Sea boundary region in the 'vicinity of Point Barrow, Alaska. Several reports were later published in connection with assessment of the offshore environment prior to oil development (Hulsemann, 1962; Wacasey, 1975; Wagner, 1977; Carey & Ruff, 1977). The most complete description of the bivalve fauna of the southwest Beaufort Sea was published by Bernard (1979). The present paper describes the coastal bivalve fauna (5-25 m depth) in the southwestern Beaufort Sea and for the first time reports patterns in numerical density, species diversity, compositional similarity, and feeding type found there.

The study region lies on the inner Alaskan shelf seaward of the barrier islands (Figure 1). The shallow area is subject to intense seasonality with major changes in insolation, ice cover, salinity, temperature, turbulence, turbidity, and sea ice gouging of the sediments (Sharma, 1979). Ice generally is present in the marginal ice zone along the southern boundaries of the Arctic Ocean from late September through early June; it attains a maximum thickness of 1.5-2.0 m (Kovacs and Mellor, 1974). The freezing and thawing sea ice cover and run-off from adjacent rivers during the summer melt season significantly affect the coastal water mass characteristics.

They decrease the salinity to as deep as 20 m, the upper limit of the pycnocline (Sharma, 1979).

Dense pack ice in the Southwestern Beaufort Sea prevents waves and wave-induced turbulence in the winter (Squire & Moore, 1980). In summer the scattered, open pack in the marginal sea ice zone and-the limited fetch of open water dampens the generation of significant waves. Erosive wind-driven currents on the inner shelf are brief (Wiseman, et al., 1974), and are generally westward-flowing on the inner shelf during the summer open water season (Mountain, 1974; Short, et al., 1974; Barnes & Reimnitz, 1974). Tidal amplitude is small and tidal currents are weak, though sea level variations caused by storms occasionally produce significant bottom currents (Matthews, 1971, 1980).

This shallow area is subject to seasonal variations in ice gouging of the sea floor. The deep keels of ice pressure ridges impinge on the bottom and move sediments creating patchy distributions (Barnes & Reimnitz, 1974; Reimnitz & Barnes, 1974). The highest frequency of scouring occurs in water depths of 20-40 m (Barnes, McDowell & Reimnitz, 1978).

MacGinitie's (1955) suggestion that the Beaufort Sea continental shelf was an homogeneous "unit environment" with benthic species uniformly distributed throughout the region has never been critically examined. Our objective was to determine if the bivalve mollusc fauna is evenly distributed throughout the coastal zone, or whether the faunal distributions are correlated with depth, sediment type or other environmental characteristics.

MATERIALS AND METHODS

Benthic macrofauna and sediments were sampled with a 0.1 m^2 Smith-McIntyre bottom grab (Smith & McIntyre, 1954) aboard the R/V ALUMIAK and the USCGC GLACIER during August and September 1976. The sampling strategy was designed to determine possible large scale faunal patterns related to depth and longitude on the inner continental shelf. The transects were normal to the coastline and located equidistant along the shelf at Point Barrow (BRB), Pitt Point (PPB), Pingok Island (PIB), Narwhal Island (NIB), and Barter Island (BAB) (Figure 1). Five biological grab samples were collected from all stations, 'which were located at 5 depth intervals between 5 and 25m on each transect (Table 1). Three stations (PIB20, PIB25, and NIB20) could not be occupied by either vessel because of heavy sea ice. The full sample set was 89 quantitative samples from 22 stations. Subsamples from an additional grab were generally taken at each station and analyzed by hydrometer for particle size and by LECO induction furnace and carbon determinator for organic carbon.

On board ship the grab samples were measured for volume, and only those with a minimum of 5.5 1 of sediment and an unwashed appearance were retained for quantitative analysis. The sediment was screened through a cascading multiple sieve system (Carey, et al., unpublished ins.) with a minimum aperture size of 0.42 mm, and the retained samples were preserved in 10% formalin neutralized with sodium borate. In the laboratory, the samples were stained with rose bengal and the large macrofauna (>1.0 mm) were picked from the sieved material under a dissecting microscope. The bivalves were identified by P.H. Scott.

RESULTS

Density and Species Richness

A total of 5,000 bivalve individuals representing 31 species were collected (Table 2). The bivalves comprised 19.8% of the numbers of benthic macrofauna >1.0 mm. Most of the numerically dominant species were found stall depths with two notable exceptions. *Boreacola vadosa,* the most abundant species, was collected only inshore at depths of 5, 10, and 15 m; 98% of the individuals were recorded from one station (PPB05). *Cyrtodaria kurriana* was found exclusively at 5 m. This limited distribution of *C. kurriana* concurs with previous reports by Wagner {1977) and Bernard (1979). Sixty-four percent of the stations contained fewer than 200 bivalve individuals per m^2. Total species numbers per station were generally low and varied from a high of 14 (PPB05) to a low of 1 species per station at NIB05 (Table 1).

Small scale spatial variation in bivalve density was evident between grabs. Frequently the variation spanned an order of magnitude in numbers of individuals per grab at a station. Large-scale differences exist between stations with a range of 1 to 2,454 individuals per station. Since the Smith-McIntyre grab is not an effective sampling device with which to elucidate small-scale patterns of benthic distribution (Jumars, 1976), differences between grabs might easily represent sampling bias. For this reason the numbers of individuals per grab at each station were combined, and the station data were analyzed to determine whether differences in total abundance correlated with depth or with transect (longitude). A two-way analysis of variance for the log-transformed number of bivalves indicates no significant difference either by depth ($F=0.793$, $P=0.55$) or by transect ($F=1.654$, $P=0.22$). The test is conservative because the interaction and error terms were combined.

The five grabs per station were again combined in an analysis to consider large-scale variation in species numbers. To include the relationship-between numbers of individuals sampled and the number of species, expected species numbers [$E(S_n)$] were calculated according to Hurlbert (1971) along with their associated variance (Heck, et al., 1975). The distribution of individuals per species for each of the 22 stations was used in calculating $E(S_n)$; 30 was chosen as the equivalent number of individuals (n) at which to compare species richness because all but four of the stations (BRB15, BRB20, PIB05, NIB05) then could be included in the analysis. Although the underlying distribution of species and individuals can affect the calculation of $E(S_n)$ and the resulting comparisons (Peet, 1974), examination of expected species curves suggests that $E(S_{30})$ is a valid measure of richness of the fauna. Two-way ANOVA with combined error and interaction terms indicate no significant difference in species richness either by depth ($F=1.339$, $P=0.31$) or transect

(F=2.301, P=0.11). No significant large-scale variations in the numbers of species were apparent for the area studied.

Compositional Similarity

Lack of systematic" variation in the total number of bivalve individuals as in the number of species does not preclude marked differences in species composition across the region. Compositional similarity was analysed by: (1) numerical classification with a similarity analysis and clustering methodology, and (2) an analysis of expected taxa shared derived from a probabilistic hypothesis. Species groups were studied by these fundamentally different approaches to determine if distinct bivalve assemblages were distributed either by transect (longitudinally) or by station across the narrow environmental gradient, and to contrast the two statistical techniques.

Numerical Classification

Similarities between all pairwise station and species comparisons were calculated using Jaccard's (1908) index. The similarity values were then clustered by a single-linkage algorithm (Anderberg, 1973). The one major species group that clustered at a Jaccard similarity greater than 0.5 is indicated in Table 2. The station-by-station comparison based on species composition is displayed as a dendrogram (Figure 2).

In the species by species comparisons one group of twelve bivalve species occurred with similarities greater than 0.5; it appears to represent the numerically abundant species in the study area (Table 2). Upon inspection of feeding type and depth distributions (Table 2), no biologically meaningful explanations can be deduced for this statistically-derived large species group. Five stations (NIB10, PPB10, PIB10, BAB15, and BAB10) at shallow depths and two (BAB25 and BAB20) in deeper water clustered as two groups, indicating a partial relationship with depth. However, no other depth-related groups were present with Jaccard similarities greater than 0.5. These results may indicate that the sample size and/or the range of environmental conditions were not large enough to elucidate species distributions by depth. However, no general patterns that included the majority of either species or stations were indicated by this technique.

The difficulty with the above procedure, and with the use of most similarity indices and clustering techniques has been the lack of a null hypothesis against which results may be tested (Connor & Simberloff, 1978; Raup & Crick, 1979). For the Beaufort Sea bivalves, groupings of species or stations must be judged on whether they represent real differences in mollusc distributions by arbitrary criteria, i.e. Jaccard similarities greater than 0.5. Recognition of these groups rests on the differences in the Jaccard or other indices and assumes an objective meaning, but this cannot be demonstrated (Connor & Simberloff, 1978; Simberloff & Connor, 1980).

Expected Taxa Shared

The arbitrary nature of similarity indices and clustering strategies has led to of various alternative approaches for viewing compositional similarity, many based on a probabilistic hypothesis (Harper, 1977; Simberloff, 1978; Raup & Crick, 1979). A null hypothesis was chosen to test whether the bivalve distributions in the Beaufort Sea conformed to a model representing stochastic persistence and random dispersion of species. Null Hypothesis I of Connor & Simberloff (1978) states that the observed number of species in common between two stations is not more than would be expected if the species composition was determined by randomly assigning species from a "common pool." The 31 bivalve species in this study are considered to represent a reasonable species pool; however, to propose that all 31 are equally likely to inhabit and to survive at any station in the Beaufort Sea is simplistic. It is important, therefore, to interpret results of the expected species analysis in the light of the assumption of ubiquitous distribution of all species of bivalves.

Table 3 summarizes the results of the compositional similarity test for the shallow Beaufort bivalve fauna, first by a pairwise comparison of all stations and second by station comparisons partitioned separately by depth and transect. Based on the calculations of expected taxa shared (E_ts) (Connor & Simberloff, 1978), 35% of all pairwise station comparisons had significant numbers of abundant species in common ($P<.05$) (Table 3-A). If in 50% of all pairwise station comparisons the number of observed taxa shared (O_ts) is greater than the computed expected value, the null hypothesis should be rejected (Hendrickson, 1981). The majority of stations under study (65%) contained more observed taxa shared (O_{ts}) than would be expected by chance, and the null hypothesis was rejected by this conservative test (x^2=47.73, $p<.005$).

To determine whether any one transect or depth can account for the differences between observed and expected species in common, station comparisons were partitioned by depth and transect (Table 3-B). In all but two of the partitioned analyses the null hypothesis is again rejected. Species in common between stations are greater than expected. For *only* the 5 m stations and the Pingok Island transect station comparisons, the null hypothesis is not rejected. This result is most likely due to the general trend of small numbers of species and individuals per station, especially at 5 m. Station PPB05 is an exception and has an anomalously high numerical density and species richness; this result distorts the total number of individuals and total species collected for the 5 m stations (Table 2). Overall, the distribution of the shallow Beaufort bivalve fauna does not appear to be solely the result of the stochastic persistence and dispersal of equi-probable species from a limited species pool. In all cases there is a significant proportion of stations that have more species in common than would be expected under the null hypothesis of random dispersal and survival.

Feeding Strategy

A study of feeding types from the inner Beaufort Sea shelf stations was undertaken to attempt to explain this non-random distribution of the coastal bivalves among the stations. We sought insight about faunal-environmental interactions at the inner margin of the marine environment where the gradients of many physical characteristics are generally steep, and we argued that a study of feeding types could yield distributional patterns of a more functional nature than groupings based on taxonomy alone.

Species were classified either as deposit or suspension feeders based on their functional morphology, information from the literature, and direct observation of the gastrointestinal tract contents of the most abundant species. Deposit feeders included all eleven protobranchs and the four Macoma species (Table 2). The remaining species were considered suspension feeders; however, feeding behavior for several species, e.g., Axinopsida orbiculata, remains questionable without direct observations. The sedimentary gut contents of Portlandia arctica and Macoma calcarea concurred with data reported in the literature for other members of their respective families (Yonge, 1939, 1949; Brafield & Newell, 1961). Liocyma fluctuosa contained a wide range of food items that was derived from suspension feeding in agreement with Ansell's (1961) findings for other members of the Veneridae. Our studies demonstrated that Boreacola vadosa, presumably a suspension feeder, had ingested resuspended flocculent material that included juvenile molluscs and terrestrial plant material. This overall classification divided the total number of bivalve species roughly in half (Table 2), although over 75% of all individuals were suspension feeders.

The percentages of suspension and deposit feeding species remained relatively constant by depth and transect, but there was a dramatic change in the relative proportions of individuals in suspension and deposit feeding categories with depth (Table 4). The innermost stations with high percent sand (65-97%) had a higher proportion of suspension feeding individuals (93%). Conversely, there was a trend toward greater numbers of deposit feeding bivalves with increasing depth, from 7% at 5 m to 85% at 25 m. Densities of bivalve feeding groups were associated both with depth ($X^2=1440.47$, $P<.005$) and transect ($X^2=186.6$, $P<.005$). There was a significantly positive correlation of deposit feeding individuals with increasing depth (Kendall's tau=0.30, $P=.026$).

Numerous studies demonstrate the effects of particle size and the resulting properties of sediments on the distribution and abundance of benthic macrofaunal species and feeding types (e.g. Sanders, 1958; Rhoads & Young, 1970; Franz, 1976; Coleman & Cuff, 1978). The shallow Beaufort sediment samples were analyzed for percent clay, silt, sand and gravel. Correlations (Kendall's tau) between sediment type and feeding type were calculated. Deposit feeder density was negatively correlated with percent gravel ($P=.003$) and with percent sand ($P=.048$). Positive correlations were found with deposit feeders and percent silt ($P=.004$) and clay ($P=.048$). No significant correlations between filter feeder density and sediment type were found. Negative correlations were found between percent sand with depth (P=.001) and positive correlations between depth and percent silt (P=.004) and between depth and percent clay (P=.001).

DISCUSSION

Results indicate that the bivalve fauna of the southwestern Beaufort Sea is broadly distributed throughout the region. There-are no strong spatial or depth patterns in overall abundance, species richness, or species composition. However, some of the fauna is reacting to depth-related features as demonstrated by the significant differences in the relative abundance of one of the functional feeding groups by depth.

In a study that involved 76 species of living bivalves and gastropod from a broad depth range (3-539 m) in the"southeastern Beaufort Sea, Wagner (1977) concluded that depth was the major controlling factor. Specific environmental features that were correlated with depth could not be identified with the techniques used in that study. Of the 10 species within the depth zone of our study that Wagner designated as depth indicators, we collected 3 species: Cyrtodaria kurriana, Macoma calcarea, and Liocyma fluctuosa (Table 2). Depth-related environmental factors on the shallow shelf that control species distributions, therefore, probably extend throughout the Beaufort Sea.

Density and Species Richness

in spite of the harsh environment in the Arctic Ocean in the nearshore depth zone sampled, 31 living species of bivalves occur with densities as high as 3,200 individuals/m^2 (mean density

$300/m^2$). MacGinitie (1959) reported only 13 species in a comparable depth zone at Point Barrow. Wacasey (1977) sampled 12 species in the 5-25 m zone in the eastern Beaufort Sea, while a study similar to ours in the nearshore Western Beaufort (4-23 m) yielded only 9 living bivalve species (Hulsemann, 1962). Higher estimates of the species richness were reported by Wagner (1977) who found 27 living bivalve species from 6-35 m in the eastern Beaufort. The most comprehensive report of Beaufort bivalves (Bernard, 1979) reported 20 species at depths of 25 m or less. In that publication based largely on Oregon State University samples the nearshore region was poorly represented.

Comparison of density and species richness between the exposed arctic coastline and more temperate coasts is illuminating. The arctic has a rich bivalve fauna and little wave activity, whereas the shallow zone (5-25 m) of the northeastern Pacific along the open coasts of northern California, Oregon, and Washington has significant wave activity throughout the year (Clifton, et al., 1971; Sternberg & McManus, 1972) and supports a limited bivalve fauna. Nelson, et al. (1981) report bivalve species from Oregon in densities generally less than $240/m^2$. Lie & Kisker (1970) sampled 5 species in shallow water off the Olympic Peninsula, Washington. The above areas were found to have an homogeneous sediment structure of over 95% sand. Boesch (1972) reported similar low diversity along the open coast of Virginia. The habitat in this region was predominately coarse sands and shell material which was subject to intense wave activity.

Boesch (1972) compared his findings in Virginia to those of Lie & Kisker (1970) on the open Washington coast. He also agreed that the macrobenthos was "predominately physically controlled by wave energy" in both areas. Persson '(1983) reported 6 bivalves species off the open coast of the southern Baltic Sea and concluded that reduced " species numbers at 5 m depth "might be due to increased exposure." Wave height in the southern Baltic is generally less than 3 m, and wave-induced bottom turbulence affects sediments to depths of 6 m.

Protected marine waters with heterogeneous and finer sediments generally harbor more species of bivalves than shallow, open-coast habitats. Sanders (1958) reported 10 species of bivalves in Buzzards Bay, Massachusetts, at depths of 10 to 20 m in muddy to sandy sediments. Lie (1968) occupied four stations with depths beteen 9 and 25 m in sheltered environments of Puget Sound, Washington where sediments were predominately fine sands. Forty bivalve species were identified from these Puget Sound stations, with average densities of 560 individuals/m^2.

Compositional Similarity - Feeding Strategy

Species and station groupings generated by similarity analyses did not provide uniform depth-related patterns (Figure 2 and Table 2). However, the bivalve species distributions have higher similarities than one would expect by random associations (Table 3). There is a pattern of distribution based on feeding strategy that appears to exist in the nearshore arctic bivalves. Limited by practical considerations in measurement of environmental parameters, we chose sediment type and station depth as possible causes of the observed patterns. Several authors have found these to be poor descriptors of nearshore molluscan distributions (Eisma, 1966; Pearson, 1970; Gage, 1974). Nonetheless, several statements can be made regarding shallow water, arctic bivalve distributions. From-5 to 25 m depths, silt and clay percentages tend to increase, although sediment types tend to be patchy in distribution. Correspondingly, numbers of deposit feeding species and individuals increase with increased silt and clay. Suspension feeders constitute the major proportion of bivalves in shallow sandy stations, although no statistically significant correlations were found. The sediment patchiness may partially explain the lack of general station grouping by depth. Hickman & Nesbitt {1980) found similar distributional patterns over a wider depth range in the molluscs of the Gulf of Alaska. As the depth and silt/clay percentages increased they reported a decrease in the proportion of suspension feeders and an increase in the proportion of deposit feeding, protobranch bivalves.

Environmental influence

The data suggest that the increase in silt and clay fractions of sediment at the deeper stations supports the greater proportion of deposit-feeding bivalves there (Sanders, 1958). However, we did not find the distinct zonation of benthic species that Oliver, et al. (1980), Massé (1972), Field (1971) and others have described in this transitional zone that lies between the turbulent surf zone and the deeper continental shelf beyond reach of average surface waves. In the southwestern Beaufort Sea there is a gradient in sediment particle size, though it appears less marked and the transition zone narrower and shallower along the open arctic coast then off the open west coast of the continental United States (Oliver, et al., 1980; Hogue, 1982).

The diminished and infrequent wave disturbance of the nearshore Beaufort Sea is likely to be a major cause of the broad distributions and the lack of clear vertical zonation of the bivalve species. Wave-generated bottom turbulence has been deduced as an explanation for patterns of distribution and abundance in the inner shelf environment for megabenthos (Davis & VanBlaricom, 1978), macrobenthos (Day, et al., 1971; Field, 1971; Christie, 1976; Rees, et al., 1977; McCall, 1977; Oliver, et al., 1977), and meiobenthos (Hogue, 1982). The data of Oliver, et al. (1980) suggest that sediment instability is caused by wave turbulence off northern California. However, in the Beaufort Sea the decrease in species richness at 5 m is probably caused by run-off and ice-related salinity changes rather than wave action.

The above statistical analyses have demonstrated that the 31 species of bivalve molluscs studied on the inner southwestern Beaufort Sea shelf are generally distributed from 5 to 25 m depth. We suggest that MacGinitie's hypothesis for uniform species distributions is upheld in this nearshore environment and that its explanation is low wave turbulence. It remains to be seen whether other major taxa also are distributed broadly in this transitional zone. Beyond this shallow environment there is a tendency for sublittoral megafaunal and macrofaunal species to have broad depth distributions across the shelf, but benthic species groups can be assigned to depth zones '(Carey, et al., 1974; Carey & Ruff, 1977, Bilyard & Carey, 1979). Beyond shelf depths the vertical distributions of species become narrower and there is a strong correlation with depth. Therefore, MacGinities "unit environment" is likely to be found only on the inner continental shelf.

Statistical Analysis

While a similarity analysis of the species data yielded several depth-related groups of stations, the results were not consistent and could not be-evaluated for statistical significance. On the other hand, the test for randomness of the data by transect and depth against an expected species null hypothesis demonstrated that there were large numbers of shared taxa between stations. It was the analysis of the biological functional feeding groups, however, that provided the trends in depth in relative abundance among species. This result pointed out the importance of biological information.

Summary and Conclusions

No significant large scale variations were found in the number of species of bivalve molluscs in the southwestern Beaufort Sea i-n the nearshore environment of 5 to 25 m depth. There were no general patterns of species distributions by depth or transect. Therefore, MacGinitie's hypothesis of uniformly distributed benthic species appears to be upheld for the coastal bivalve molluscs.

The majority of stations contained more species in common than would be expected by chance alone; therefore, the distribution of bivalve species does not appear to be the result of stochastic persistence.

Patterns of relative abundance of species are probably caused by feeding type-sediment interactions. Proportionally more deposit feeding organisms live at the deeper stations that correlated with increased silt-clay fractions in the sediment.

Species richness and numerical density are higher on the arctic inner shelf than at similar depths on temperate open coastal environments. Diminished bottom turbulence caused by low surface wave activity is a possible explanation for this phenomenon.

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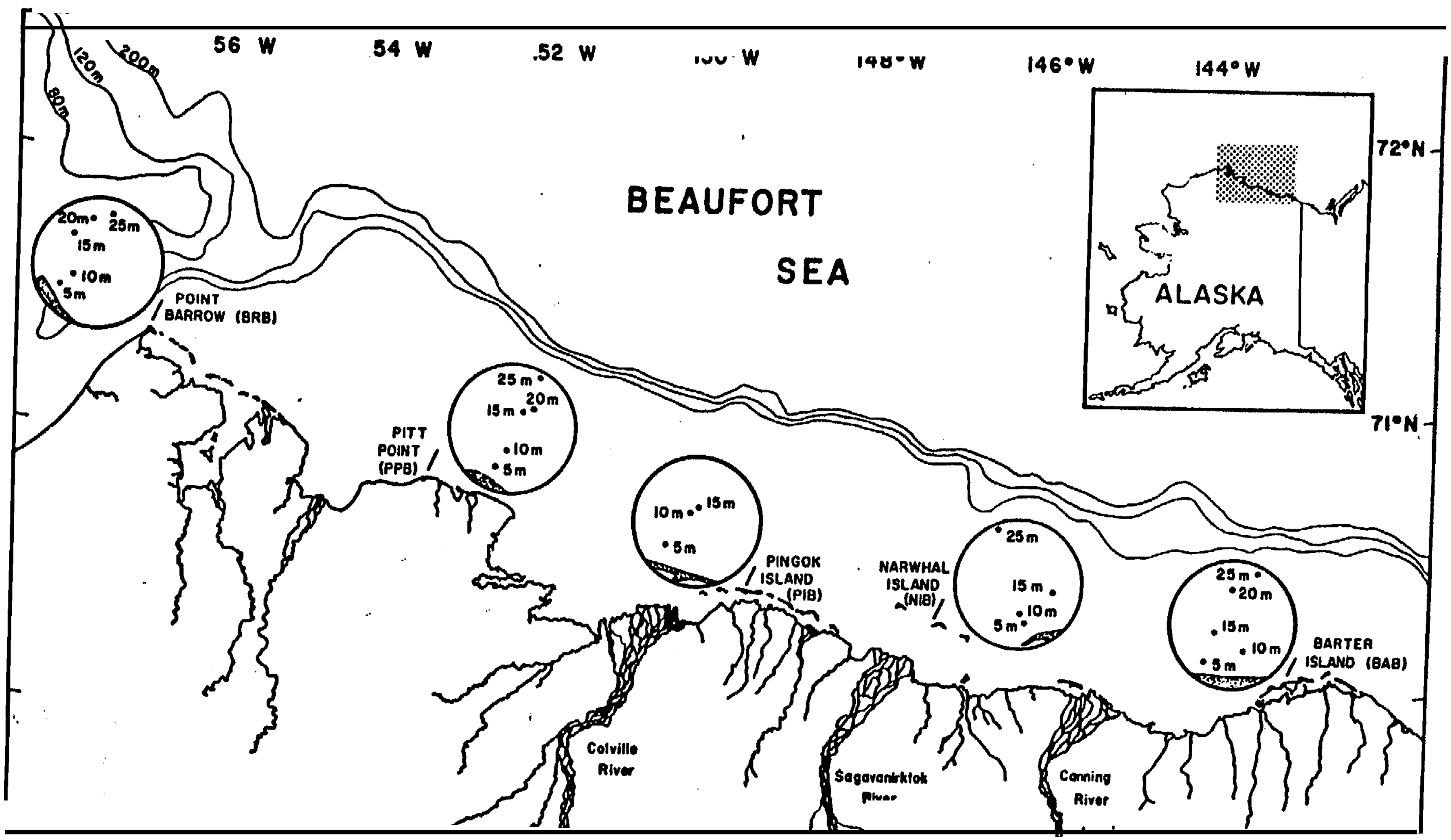
ACKNOWLEDGEMENTS

We thank P.A. Montagna for assistance in the laboratory and field, and R.E. Ruff and L. Yee-Downs for their assistance in the laboratory. F. Bernard and E.V. Coan aided in taxonomic matters, and S. Naidu analyzed the sediments. E.W. Hogue, R.E. Ruff, G. Braun, E.V. Coan, F.G. Hochberg, J.N. Nybakken, B. Profaut, B. Roth, C.B. Miller, and W.G. Pearcy contributed helpful comments during development of the manuscript. We acknowledge the kind assistance of the officers and crew of the R/V ALUMIAK and the USCGC GLACIER. This study was funded by the Bureau of Land Management through interagency agreement with the National Oceanic and Atmospheric Administration as part of the Outer Continental Shelf Environmental Assessment Program.

Figure Legends

Figure 1. Location map of the northern coast of Alaska showing the station transects in the southwestern Beaufort Sea and the individual station locations (circle insets). Scale - circle inset diameter: BRB and PIB=10.5 km; PPB=29.8 km, NIB and BAB=6.4 km.

Figure 2. Single linkage clustering of Jaccard station similarities for bivalve molluscs in the SW Beaufort Sea.



56 W
54 W
52 W
148° W
146° W
144° W
72° N
71° N
200m
120m
80m
BEAUFORT
SEA
ALASKA
20m
25m
15m
10m
5m
POINT
BARROW (BRB)
25 m
20m
15 m
10m
5m
PITT
POINT
(PPB)
10m
15m
5m
PINGOK
ISLAND
(PIB)
NARWHAL
ISLAND
(NIB)
25m
15 m
10m
5m
25m
20m
15m
10m
5m
BARTER
ISLAND (BAB)
Colville
River
Canning
River

Figure 1.

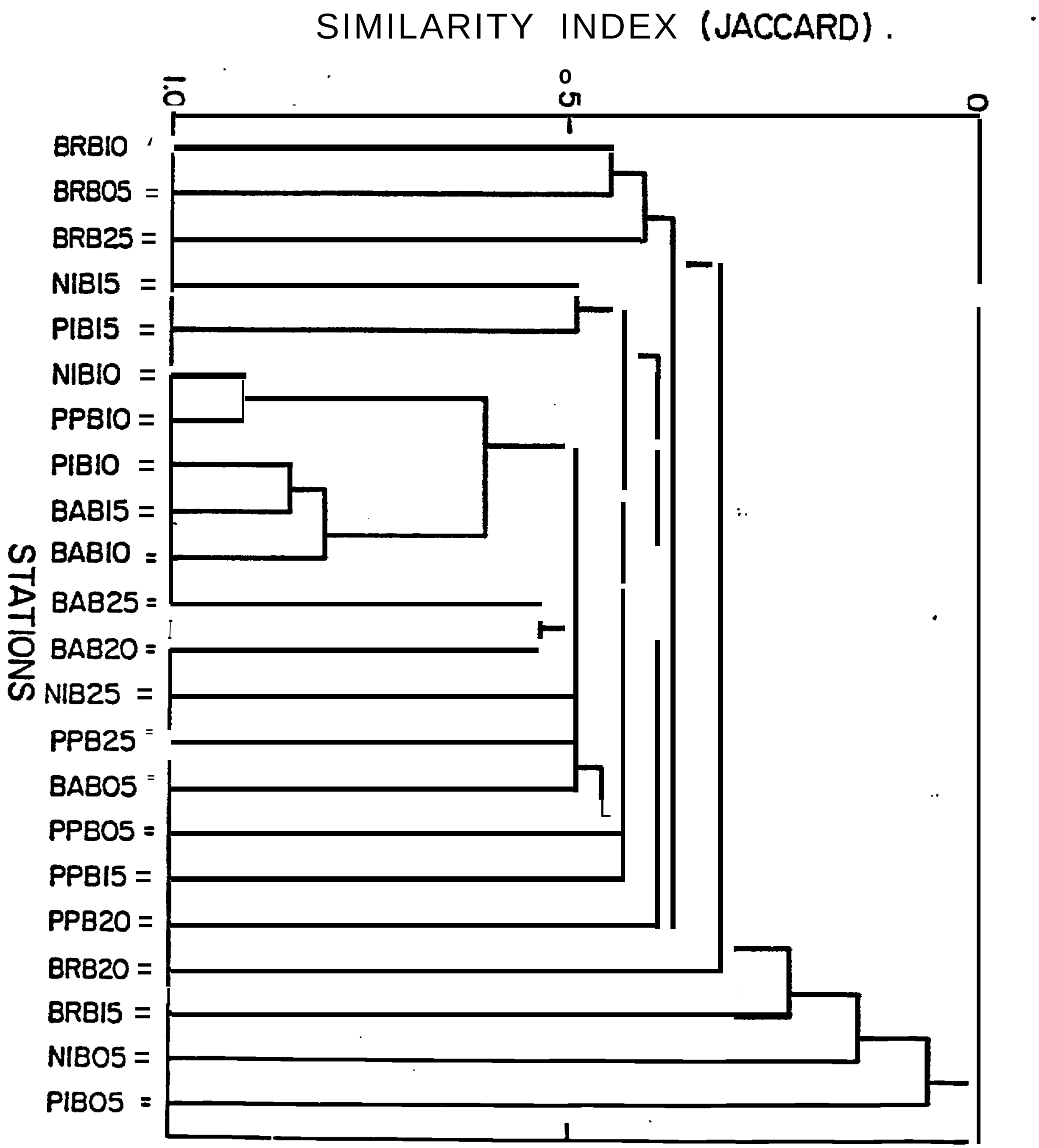


Figure 2. Single linkage *clustering* of **Jaccard** station **similarities.**

Table 1. Environmental parameter, bivalve abundance and bivalve feeding types in the Beaufort Sea coastal zone.

Transect	Depth (m)	Environment: Sediment Type	Gravel %	Sand %	silt %	Clay %	% Organic Carbon	Bivalve Fauna: # of Species	# of Individual	% Suspension Feeders	% Deposit Feedera
Pt. Barrow (BRB)	5	Sand	1.4	96.6	1.1	0.9	0.10	4	44	100	0
	10	Silty sand*	--	--	--	--	--	11	215	88	12
	15	Sandy silt*	--	--	--	--	--	2	5 .	20	80
	20	Sandy silt*		--	--	--	--	3	22	45 '	55
	25	Sandy silt*	--	--	--	--	0.47	5	58	14	86
Pitt Point (PPB)	5	Silty sand	0.0	38.0	39.2	22.8	0.81	14	2454	94	6
	10	Silty sand	0.0	65.8	26.3	7.8	0.17	10	243	60	40
	15	Clayey silt	0.0	71.0	19.2	9.8	1.0	4	40	2	98
	20	Clayey silt*	0.0	8.1	51.2	40.7	--	4	98	1	99
	25	Clayey silt	--	--	--	--	0.78	10	217	4	96
			0.0	4.3	49.1	46.6					
Pingok Island (PIB)	5	Sand	0.0	73.2	16.9	9.9	0.09	2	4	0“	100
	10	Silty sand	0.0	53.3	38.8	7.9	0.03	11	422	54	46
	15	Sandy silt*	--	--	--	--	.-	12	215	73	27
Narwhal Island (NIB)	5	Gravel-sand	15.9	71.8	6.4	5.9	<0.01	1	1	100	0
	10	Sand	0.3	85.8	7.0	6.9	0.08	7	53	92	8
	15	Gravel-sand	27.0	54.0	10.3	8.7	<0.01	12	3 5	66	34
	25	Sand-silt-clay	9.6	27.9	27.7	34.8	0.15	12	36	31	69
Barter Island (BAB)	5	Sand-silt-clay	0.0	29.2	38.6	32.2	<0.01	5	19	74	26
	10	Sand	0.0	92.5	4.5	3.0	0.03	7	97	60	40
	15	Silty sand	0.0	64.8	22.5	12.7	0.17	10	378	66	24
	“ 20	Silty sand	0.0	47.0	25.7	27.3	0.31	13	24S	73	27
	25	Sand-silt-clay	0.0	37.6	24.8	37.6	0.34	8	99	“ 33	67

•Classified from field notes

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Table 2. Distribution of bivalve species by depth and feeding type (S=suspension feeder, D=deposit feeder). Species are ordered by increasing depth. Those taxa which clustered as one group at a Jaccard similarity greater than 0.5 are indicated by*. Taxonomic nomenclature follows Bernard (1979).

Species	Feeding Type	Mean Number per m² Depth (m) 05	10	15	20	25	Total Number Collected
**Axinopsida orbiculata*	S	91	146	80	106	1	956
* *Portlandia arctica*	D	14	1(I4	45	84	60	774
**Liocyma fluctuosa*	S	130	87	46		<1	659
**Macoma calcarea*	D	49	22	27	11	29	313
**Arctinula greenlandica*	S	<1	3	8	'9	15	89
**Pandora glacialis*	S	<1	3	13	1	1	49
Cyrtodaria kurriana	S	63					157
Nuclulana minutia	D	<1					3
Cyclocardia crebricostata	S	<1					2
Mysella planata	S	<1	1				7
Hiatella arctica	S	<1	<1			1	9
**Astarte montagui*	S	1		32			87
Boreacola vadosa	S	640	15	<1			1640
Serripes groenlandicus	S	17	5	<1			57
**Thracia devexa*	S	<1		1			7
Yoldia hyperborea	D		<1				2
Yoldia myalis	D		<1			<1	6
Portlandia sp. A	D		<1	1			8
Lyonsia arenosa	S		2	5			18
**Macoma inflata*	D		<1	1			8
**Macoma moesta*	D		9	.3		3	58
**Nucula belloti*	D		<1	<1	.4	5	37
Mya pseudoarenaria	S		5	<1	1	<1	18
**Crenella decussata*	S			<1	<1		3
Nuculana radiata	D			<1	<1	1	7
Portlandia frigida	D			<1	<1	<1	4
Macoma loveni	D			<1	<1	<1	3
Nuculand pernula	D				<1	1	6
Portlandia lenticula	D				<1	2	8
Mysella tumida	S					<1	1
Thracia myopsis	S					1	4
Number of species		15	18	20	14	18	31
Number of individuals collected		2,522	1,030	673	365	410	5,000

Number of Stations

le 3. Summary of results obtained under Null Hypothesis I (Connor & Simberloff, 1978). The partitioned analyses (B) are comparisons based on stations from a particular depth or transect (longitude) against all other stations in the study area.

parisons	Total No. Pairwise Comparisons	OBS>Exp	OBS>Exp (P<.05)	OBS<Exp	OBS<Exp (P<.05)	OBS=Exp (P<.05)	CHI-Square	P
Total analvsis								
stations	231	168	81(35%)	63	0	151{65%)	47.73	<.005
Partitioned analyses								
depth								
5	95 -	45	17 (18%)	50	0	78 (82%)	0.26	>.05
10	95	81	44 (46%)	14	0	51 (54%)	47.26	<.005
15	95	73	30 (32%)	22	0	65 (68%)	27.38	<.005
20	60	46	24 (40%)	14	0	36(69%)	17.06	<.005
25	78	61	26(33%)	17	0	52 (67%)	24.82	<.005
Transect								
BRB	95	64	20 (21%)	31	0	75 (79%)	11.46	<.005
PPB	95	77	42 (44%)	18	0	53 (56%)	36.63	<.005
PIB	60	35	17 (28%)	25	0	43 (72%)	1.66	>.05
NIB	78	49	23 (29%)	29	o"	45 (71%)	5.12	<.025
BAB	95	78	43 (45%)	17	0	52 (55%)	29.16	< .005

Table 4. Bivalve feeding types.

A. Percent feeding type by depth and by transect. Based on total number of individuals collected at each station.

Depth(m)	Total # of Individuals	% Suspension Feeders	% Deposit Feeders
5	2,539	93	7
10	1,030	57	43
15	673	70	30
20	365	52	48
25	410	15	85
Transect			
Pt. Barrow	344	76	24
Pitt Point	3,052	81	19
Pingok Island	641	60	40
Narwhal Island	125	67	33
Barter Island	838	68	32

B. Percent of species: feeding type by depth and by transect.

Depth(m)	Total # of Species	% Suspension Feeders	% Deposit Feeders
5	15	80	20
10	18	55	45
15	20	55	45
20	14	36	64
25	18	44	56
Transect			
Pt. Barrow	12	58	42
Pitt Point	20	60	40
Pingok Island	16	56	44
Narwhal Island	18	56	44
Barter Island	18	50	50